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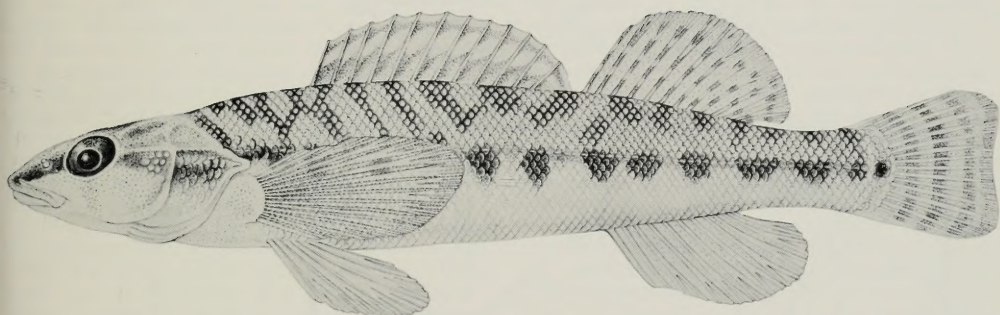


NATURAL HISTORY
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THE LIFE HISTORY OF THE SLENDERHEAD DARTER, *PERCINA PHOXOCEPHALA*, IN THE EMBARRAS RIVER, ILLINOIS

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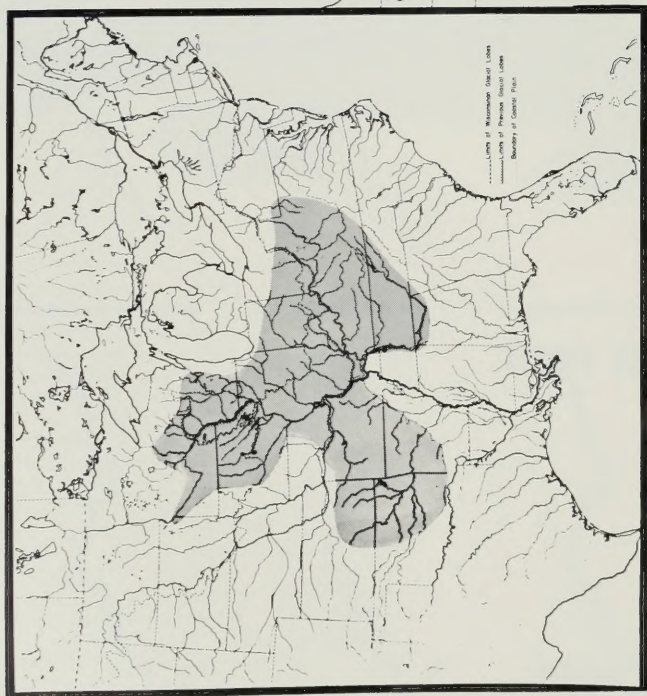
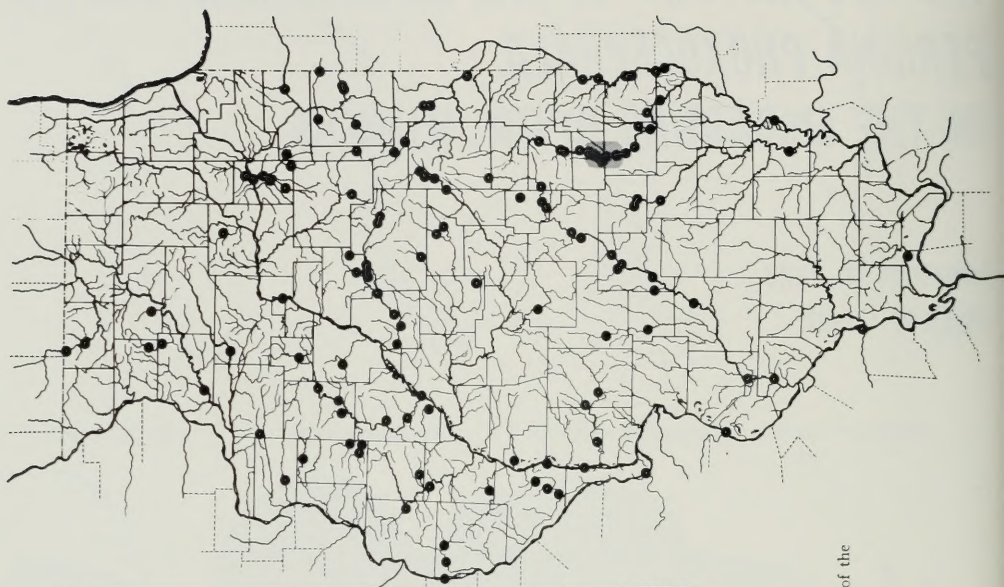


Fig. 1.—Distribution of *Percina phoxocephala* in Illinois and the total range (left) of the species. The study area is shaded on the Illinois map.

THE LIFE HISTORY OF THE SLENDERHEAD DARTER, *PERCINA PHOXOCEPHALA*, IN THE EMBARRAS RIVER, ILLINOIS

Lawrence M. Page and Philip W. Smith

THE SLENDERHEAD DARTER, *Percina phoxocephala* (Nelson), is the most widely distributed and best known of the four species assigned to the subgenus *Swainia*, which also includes *P. squamata* (Gilbert & Swain 1887), a species with a small range centered in eastern Tennessee; *P. oxyrhyncha* (Hubbs & Raney 1939), limited to West Virginia and Virginia; and *P. nasuta* (Bailey 1941), occurring in northern Arkansas, eastern Oklahoma, and southern Missouri.

Despite many references to the occurrence, relative abundance, and habitat preferences of *P. phoxocephala*, details of its life history are limited to observations made in Iowa by Karr (1963) and in Illinois by Thomas (1970). No published information is available on the life histories of the other species of *Swainia*. Because of the paucity of life-history data and the availability of a large population of *P. phoxocephala* in the middle Embarras River, a detailed study of the life history of this darter was commenced in August 1967 in conjunction with a similar study of the dusky darter, *P. sciera*. References to *P. sciera* in the following text are based on the latter investigation (Page & Smith 1970).

The slenderhead darter was described by Edward W. Nelson (1876:35) as *Etheostoma phoxocephalum* from "the Illinois [River] and its tributaries." The species (cover illustration) is a medium-sized darter, sexually mature individuals ranging from 40 to 80 mm in standard length, with a slender body and an attenuated snout. Its scales are small, the lateral-line count ranging from 60 to 80 scales. Opercles and nape are scaled; cheek squamation is variable. The breast of the female is naked, except for one or two enlarged, strongly ctenoid scales. The posterior half of the male's breast is scaled; the anterior half is naked. Dorsal spines number 11 or 12, soft dorsal rays 11–14. The anal fin has two spines and eight or nine soft rays. The gill covers are moderately conjoined.

The dorsum is light brown or straw color with darker brown vermiculations and blotches. The venter is white. Along each side of the body is a row of 10–16 rather obscure, more or less confluent, dark blotches. There

is a small, discrete, black caudal spot and a dark stripe extending from the tip of the snout backward through the eye. Usually there is no suborbital bar. The best field character is the submarginal band of bright orange in the spinous dorsal fin.

The male can be distinguished from the female at all seasons and all sizes above 25 mm standard length by a median row of enlarged specialized scales extending from the midpelvic area to the anus. During late spring and early summer the male has closely spaced melanophores over the breast and belly and on the ventral fins; the female is white below and has only a few scattered melanophores on the anal fin. The spinous dorsal fin of the male is more heavily pigmented than is that of the female, the basal portion being quite dark. For a few weeks prior to spawning the female can be recognized by its distinctly enlarged genital papilla; the genital papilla of the male is a small triangular flap.

The small young of the species can be readily distinguished from other young darters in the Mississippi River valley by the combination of a slender habitus, attenuate snout, and the characteristic dorsal spotting.

P. phoxocephala occurs from western Pennsylvania to northeastern South Dakota—although it is for the most part absent from the Great Lakes drainage—and southward to northern Alabama and southern Oklahoma (Fig. 1). The species is not found in the lower Mississippi River valley and rarely occurs in low-gradient, lowland streams anywhere within its range. In Illinois it is widely distributed and generally common, except in the northeastern and extreme southern parts of the state.

We are much indebted to Raymond T. Schaaf, Mrs. Dorothy M. Smith, Norman D. Penny, Hartley F. Hutchins, Robert O. Watson, Miss C. Catherine Huheey, and the late Robert L. Hass for aid in collecting specimens; to our entomologist colleagues Donald W. Webb and Drs. John D. Unzicker and Milton W. Sanderson for their help in identifying arthropod remains in darter stomachs; to Dr. Marvin C. Meyer of the University of Maine for identifying the leech parasite found on our *P. phoxocephala* specimens; to Harman F. Smith, Illinois State Water Survey, for providing data on the water chemistry of the Embarras River; and to our associate Dr. R. Weldon Larimore for counsel on various matters. We also thank Chief Fishery Biologist A. C. Lopinot of the Illinois Department of Conservation and his staff of

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COVER ILLUSTRATION: Adult female *Percina phoxocephala* collected in May in the Embarras River, Cumberland County, Illinois. From a drawing by Mrs. Alice Ann Prickett.

biologists for a considerable number of Illinois collections of darters.

The drawings of *P. phoxocephala* and genital papillae were done by Mrs. Alice Ann Prickett, University of Illinois School of Life Sciences Artist. Assistance in preparing the illustrations was provided by Illinois Natural History Survey Technical Illustrator Richard M. Sheets and Survey Photographer Wilmer D. Zehr. The manuscript was edited by Robert M. Zewadski, Associate Technical Editor of the Survey. Dr. David A. Etnier, University of Tennessee, served as special guest reviewer.

THE STUDY AREA

The area selected for study (the shaded oval in the lower-right quarter of Illinois in Fig. 1) extends from a gravel bar in the middle Embarras River $\frac{1}{2}$ mile north of Greenup, Cumberland County, south to a site 3 miles west of Rose Hill, Jasper County, Ill., although most of the collections were made over gravel bars at Greenup.

The Embarras River, a tributary of the Wabash River, flows through the Wisconsin end moraines in

the vicinity of Charleston and has deposited large quantities of glacial gravel and sand for the entire length of the study area. The water is well oxygenated by flowing over the many fast riffles bordering sand and gravel bars that alternate with deep, relatively quiet pools. Chemical measurements taken in the Embarras River at Camargo in Douglas County from October 1966 to April 1968 by the Illinois State Water Survey and made available through the courtesy of Mr. Harman F. Smith, indicated that water quality was unusually high and that pollution was minimal (Page & Smith 1970:5).

In the vicinity of the study area the stream could be classed as a small to medium-sized river. During low water stages the channel was only 15–30 feet wide and in riffle areas barely a foot in depth, although there were some deep pools at bridge sites and at abrupt bends in the river. During flood stages the inundated floodplain was almost 1 mile wide.

One of the principal study sites, 1 mile west of Greenup, had a variety of habitats, consisting of gravel bars and gravelly raceways, sandbars and sandy raceways, a rubble riffle, and several silt-bottomed pools.



Fig. 2.—Study area on the Embarras River $\frac{1}{2}$ mile north of Greenup, Ill.

Another site, ½ mile north of Greenup, was similar but had more extensive stretches of gravel (Fig. 2).

METHODS

Minnow-seine collections were made at 2-week intervals from August to November 1967 and at irregular intervals throughout 1968, 1969, and 1970 as material was needed to obtain information for all seasons. A total of 45 collecting and observation trips was made to the study area between August 4, 1967 and September 10, 1970.

In the field notes were made on the river and weather conditions, pigmentation of the darters, and the habitats in which specimens were captured. During the spring and early summer months, water and air temperatures were routinely recorded.

Occasionally various habitats were sampled to determine habitat preferences, but most efforts were concentrated in the channels, where the species was most easily obtained. During the winter months numerous habitats were sampled in an effort to find the overwintering habitat of the species. Obtaining specimens during the winter and during periods of high water proved difficult, and no specimens were secured during January or December. Specimens collected during the 3-year study period were distributed as follows: February, 1; March, 1; April, 1; May, 35; June, 50; July, 19; August, 16; September, 75; October, 25; November, 15.

Supplemental specimens in the Illinois Natural History Survey ichthyological collection provided information to help fill the gaps resulting from the difficulty of collecting specimens during the cold months. A total of 440 preserved specimens was examined in the study. Only the 238 specimens collected and examined from the study area were used for the growth measurements, and only collections from the study area made during the study period were used in discussions of population characteristics.

Specimens were dropped into 10-percent formalin as soon as they were captured. Later they were measured, their age and sex were determined, and details of color pattern and the presence of external parasites were noted. Unless stated otherwise, all measurements given in the text are standard lengths. Age determinations were made by counting annuli on scales removed from just above the lateral line below the junction of the spinous and soft dorsal fins.

Some specimens from each collection were dissected and examined for stomach contents, the presence of macroscopic parasites in the alimentary canal, and gonad condition. Gonads were measured, and a few were blotted dry and weighed on a chain balance. Ovaries showed significant increases in weight as the spawning season approached, but testes were too small to be weighed accurately. Ova were counted in several females. The stomachs of some potential predators of *P. phoxocephala* were examined for darter remains.

Living *P. phoxocephala* specimens were brought to the laboratory several times during the study to observe their behavior in aquaria. When it became evident that aquarium-held captives were not going to spawn, eggs and sperm were stripped from ripe adults in several unsuccessful attempts to obtain embryos.

On October 17, 1967 a quantitative sample was taken ½ mile north of Greenup with an electric seine (Page & Smith 1970:5) to estimate the composition of the fish fauna at the site and the number of individuals per areal unit of habitat.

HABITAT AND ASSOCIATED SPECIES

In the Kaskaskia River of Illinois, Thomas (1970:7) found *P. phoxocephala* to be most abundant in the middle river, rare in the headwaters, and occasional in the lower river. The moderate-to-fast current over gravel and the high riffle-to-pool ratio in the middle river were considered responsible for the increased abundance in the middle river (ibid.:7, 16).

In Ohio, Trautman (1957:545) found *P. phoxocephala* to be most common over "extensive bars and riffles which contained clean sand and small gravel that was almost free of silt." In Kansas, the species occurs "in swiftly-flowing, shallow water, over a bottom of loose gravel or of bedrock littered by stones" (Cross 1967:292). In the portion of the Embarras River used for both the *P. sciera* and the *P. phoxocephala* life-history studies, the two species were generally found occupying the same habitat, the relatively shallow, gravel-bottomed portion of the river channel. *P. phoxocephala* was somewhat less restricted to gravel than was *P. sciera* and occasionally was taken in the channel over sand.

Collections from elsewhere in Illinois have revealed more plasticity by *P. phoxocephala* in habitat choice than was exhibited by the population in the Embarras River. Specimens have been taken from small-stream riffles, large rocky riffles, and even sandy pools of large rivers. However, the abundance of *P. phoxocephala* in the middle Embarras River indicates the optimal habitat for the species to be the gravel-bottomed raceways of medium-sized rivers with moderate current.

Juvenile *P. phoxocephala* remained in the spawning habitat (shallow riffles along gravel bars) several weeks after hatching. At approximately 1 month of age the young darters moved out into the deeper water of the channel.

Page & Smith (1970:6) summarized the species diversity in a section of the Embarras River blocked off with minnow seines and sampled with an electroseine. They found *P. phoxocephala* to be the second most common darter and the 13th most common species of fish; it constituted 0.5 percent of the total fish population. Collections taken in the other study areas over a 3-year period tend to substantiate this numerical relationship between *P. phoxocephala* and associated species.

The species most commonly associated with *P. phoxo-*

cephala were *Notropis whipplei*, *N. spilopterus*, *N. stramineus*, *Pimephales vigilax*, *Ericymba buccata*, *Percina sciera*, *Hyentelium nigricans*, *Micropterus punctulatus*, and *Phenacobius mirabilis*.

REPRODUCTION

The Reproductive Cycle of the Male

Males were sexually mature and ready to spawn during the first spring following their hatching. The smallest male captured in spring was a 40-mm specimen collected on May 27, 1969; although breeding pigmentation was absent in this fish, its testes were large (6 x 1.5 mm) and it apparently was capable of spawning, as were all of the larger males collected in the spring and examined for sexual maturity.

The larger the male, the earlier the breeding pigmentation began to develop and the more intense it became by spawning time. Males 2 years old collected on May 27, 1969 were considerably darker than females and somewhat darker than 1-year-old males collected at the same time. The brown vermiculations on the dorsum were darkened in males, and in contrast to females, the breast; belly; underside of the head; and membranes of the anal, soft dorsal, and pelvic fins of the males were covered with many expanded melanophores, giving them an over-all dusky appearance (Fig. 3).

Besides the duskiest of the males, there was a pronounced color difference between the sexes in the pigmentation of the soft dorsal fin. In addition to increased melanization, the dorsal rays of males were boldly outlined with yellow; the soft dorsal fins of the females had no visible yellow pigment.

Although the width and color intensity of the yellow-orange submarginal band in the spinous dorsal fin were usually greatest in males, pronounced variations occurred in both sexes. The color varied from pale yellow to bright orange.

Pigmentation changes began in April and peaked at spawning time. The darker color of freshly captured, large males taken in the spring made them easily separable from females. Large size and more intense coloration undoubtedly enhanced sex recognition and provided older males an advantage over younger males in attracting females.

Breeding *P. phoxocephala* males did not develop tubercles. Collette (1965:577) found breeding tubercles on none of the species of *Swainia*. The genital papillae of males were small, triangular flaps which enlarged slightly as spawning neared (Fig. 4).

The testes began enlarging in late summer, and continued to enlarge until spawning time. In specimens collected on September 21, the length of the testes averaged 10 percent of the standard length; in a specimen

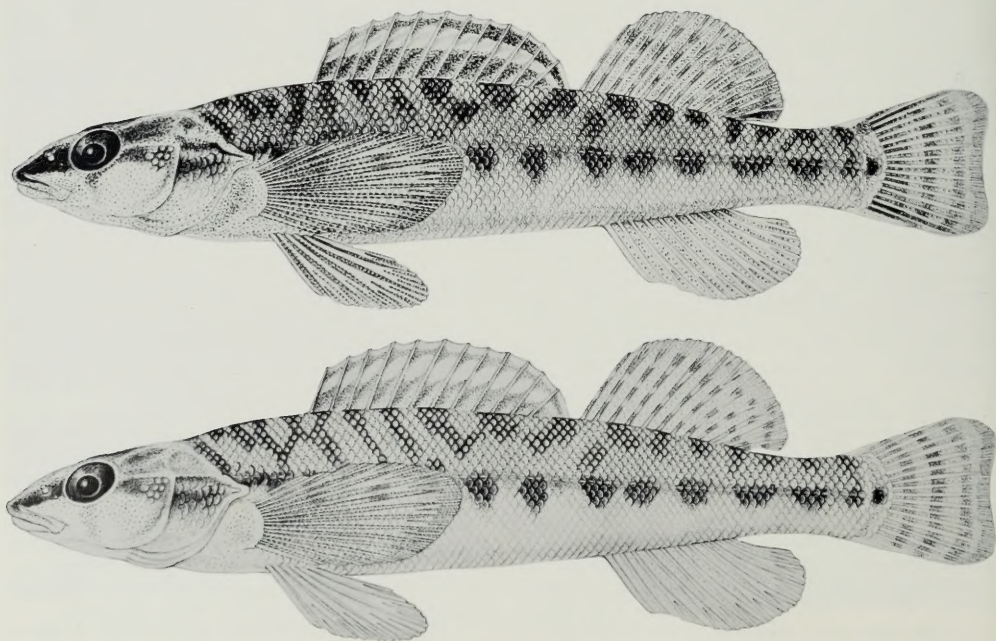


Fig. 3.—Pigmentation patterns of a 63-mm breeding male (top) and a 56-mm breeding female (bottom) *Percina phoxocephala*, both captured on May 26, 1970.

collected on October 14, 11 percent; on April 28, 19 percent; on May 27, 15 percent; and on June 8, 21 percent.

The Reproductive Cycle of the Female

No difference between the pigmentation of breeding females (Fig. 3) and that of non-breeding females was

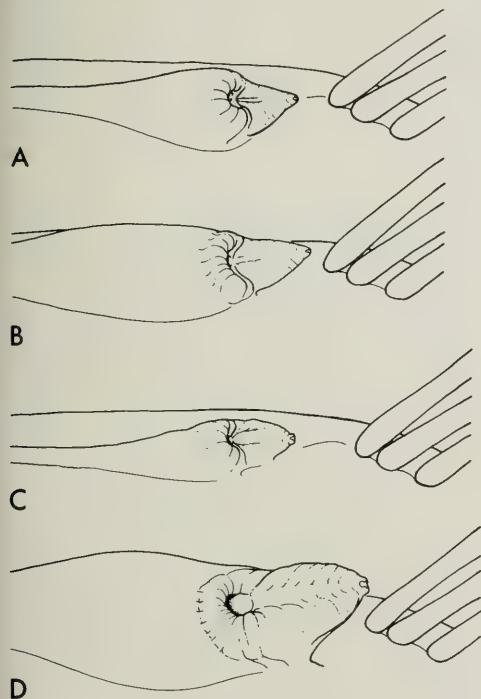


Fig. 4.—Urogenital papillae of: A, male in the fall; B, male in the spring; C, female in the fall; and D, female in the spring.

discernible. Sexual dimorphism in *P. phoxocephala* seems to be limited to the contrast between the "normal" pigmentation of *P. phoxocephala* and the pigmentation of breeding males, the difference in breast squamation, and the presence of the specialized scales on the mid-belly of males versus their absence on females.

In the spring the genital papillae of females were enlarged, striated, conical structures (Fig. 4). In the fall the papillae of females were morphologically similar but proportionally much smaller than those of specimens taken in the spring.

Females having attained a standard length of at least 42 mm were sexually mature at 1 year of age. All spring-captured females examined that were 42 mm or larger contained ova at least 1 mm in diameter and were ready to spawn. The only sexually immature spring-collected female was a 38-mm specimen collected on May 27, 1969.

The prespawning period was characterized by the differentiation and maturation of ova; the spawning act by the release of mature eggs; and the postspawning period by the absorption of the remaining ova and recovery of the ovaries. In *P. phoxocephala*, the recovery time for females was very short, and enlargement of the ovaries began soon after spawning (Table 1).

Early stages of ova maturation proceeded slowly, but as spawning time approached, development was rapid. The growth of ova was reflected in an increase in the weight of the ovaries, which, in relation to body weight, showed an exponential increase between July and the following June (Fig. 5).

As with other fishes, developing ova were easily categorized into three groups based on size and color: the smallest ova were white and less than 0.5 mm in diameter; the intermediate were between 0.6 and 1.0 mm and yellow; and the largest were 1.1–1.3 mm and yellow to orange in color.

Ova categorized as intermediate were present in a February-collected female (Table 2); large ova first appeared in April. The proportion of small ova decreased as spring approached, and the proportion of large ova increased. The number of intermediate ova

TABLE 1.—Lengths and weights of ovaries of *Percina phoxocephala* collected in different months of the year.

Collection Date	Length in mm			Weight in Grams		
	Standard Length of Female	Length of Ovary	Ovary Length as Percent of Standard Length	Adjusted Weight* of Female	Weight of Both Ovaries	Ovary Weight as Percent of Adjusted Weight
July 21, 1959	67	13	19.4	3.66	0.02	0.5
August 23, 1967	55	9	16.4	2.08	0.02	1.0
September 1, 1967	54	8	14.8	1.82	0.02	1.1
October 22, 1967	57	11	19.3	2.39	0.06	2.5
November 8, 1963	66	14	21.2	3.02	0.09	3.0
February 23, 1969	58	13	22.4	2.40	0.12	5.0
April 28, 1968	44	12	27.3	1.00	0.12	12.0
May 27, 1969	56	14	25.0	2.30	0.35	15.2
June 8, 1969	60	18	30.0	2.59	0.52	20.1

* Adjusted weight is the weight of the female minus the ovaries, stomach, and intestines.

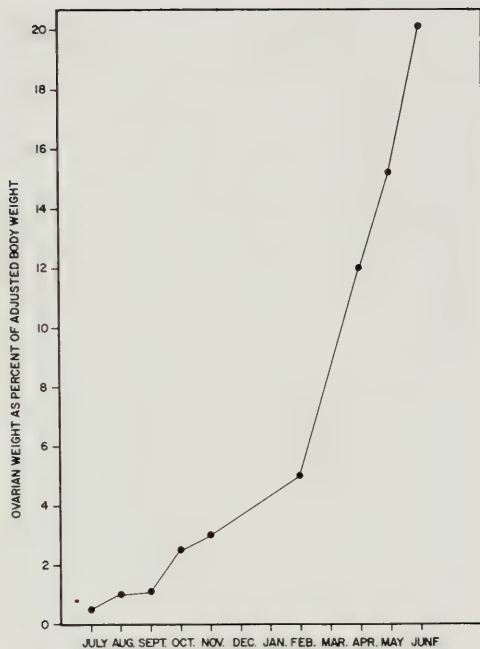


Fig. 5.—Increase in weight of ovaries in relation to body weight from the end of one spawning season to the beginning of the next.

remained between 9 and 24 percent in specimens collected after late February.

Between 500 and 2,000 ova were produced by each female in one season, but only about 10–50 percent reached mature size. If we assume that darters lay all the mature eggs, as suggested by Fahy (1954:166) and Winn (1958b:181), each female *P. phoxocephala* lays from 50 to 1,000 eggs in one season. The largest number of mature ova actually counted was 720 in a 60-mm female; the smallest number was 50 in a 45-mm female. Karr (1963:235) counted the eggs in six *P. phoxocephala* from Iowa and found a range of 186–365. Large females produced more eggs than did small females. The mean number of mature eggs in three spring-collected 1-year-old females examined during this study was 83; the mean number in six spring-collected 2-year-olds was 270.

Mature eggs stripped from ripe females were transparent and adhesive, averaged 1.3 mm in diameter, and contained one large oil droplet.

Spawning

The peak spawning period in 1969 was June 7–14, and in 1970, June 5–12. In 1968 high water prevented spring collections and presumably delayed spawning,

TABLE 2.—Differentiation and growth of ova in *Percina phoxocephala* collected in the study area.

Collection Date	Estimated Percent of Differentiated Ova	Percent of Differentiated Ova by Size Group		
		0.1-0.5 mm	0.6-1.0 mm	1.1-1.3 mm
October 3, 1967	30	100	0	0
November 17, 1963	40	100	0	0
February 23, 1969	80	81	19	0
April 28, 1968	over 90	75	17	8
April 28, 1968	over 90	80	9	11
May 4, 1968	over 90	69	16	15
May 27, 1969	over 90	59	24	17
June 8, 1969	over 90	56	23	21
July 18, 1967	over 90	42	17	41

inasmuch as the spawning habitat (shallow gravel riffles) was not available until sometime in July.

The spawning period for *P. phoxocephala* in central Illinois varies with climatic conditions and presumably may peak anytime after late May. Females heavy with mature eggs were captured at Greenup in late May in both 1969 and 1970, indicating that spawning could occur that early in the year under ideal conditions. Thomas (1970:8) collected ripe females in early August in the Kaskaskia River at about the same latitude as that of the Embarras River study area. He noted, however, that no ripe males were collected that late in the year, and it is highly improbable that spawning would occur later than early July in central Illinois.

The spawning habitat of *P. phoxocephala* is swift-flowing water 15–60 cm (½–2 feet) deep over gravel. Males move in mass into the spawning habitat well before the females do and presumably establish territories although no actual observations of territoriality were made. In 1970 males were common in the shallow water along gravel bars as early as May 29. The ratio of males to females captured in the shallow water on this date was 15:1; on June 5 it was 11:2. The fish spawned during the following week and by June 13 all adult *P. phoxocephala* had left the spawning grounds.

Spawning could neither be observed in the field nor induced in aquaria. The morphology and spawning habitat of *P. phoxocephala* suggest, however, that mating and deposition of the eggs occur in a manner similar to that described for other *Percina* species (New 1966; Loos & Woolcott 1969; Reighard 1913; Winn 1953, 1958a, and 1958b).

Juveniles remain in the spawning habitat 2–4 weeks after hatching. Several young were collected in the shallow water (15–30 cm deep) along a gravel bar in the study area where spawning was known to have occurred 2 weeks before. With the young *P. phoxocephala* (ranging from 19 to 27 mm) in the riffles were two young *P. sciera* (19 and 21 mm) and one young *P. caprodes* (33 mm). Collecting in the shallow riffle areas 2 weeks later produced no young *P. phoxocephala*.

DEVELOPMENT AND GROWTH

Development

The smallest specimen available (18.7 mm standard length, 22.4 mm total length) was collected in the study area on June 23, 1970. Presumably a product of the peak spawning period of June 5–12, the fish was estimated to be 2 weeks old. Its body proportions (Fig. 6) were essentially those of the adult, except that the head and eyes were large in relation to the size of the body. The head length was 32 percent of the standard length versus an average of 27 percent of the standard length for 10 adults. Squamation was nearly complete; the only areas lacking scales were the cheeks, opercles, nape, and the anterior two-thirds of the belly.



Fig. 6.—Two-week-old *Percina phoxocephala* 19 mm in standard length.

The pigmentation of this small specimen was weak but showed the pattern characteristic of adults. The dorsal spots, lateral blotches, band around the snout, and spots in the fins of adults were represented by concentrations of melanophores. Yellow pigment in the spinous dorsal fin indicated the beginning of the orange-yellow band characteristic of the adult *P. phoxocephala*. The lateral line was complete and fully pored. The head canals were nearly complete except for a wide medial interruption in the supratemporal canal.

Slightly larger specimens (21–23 mm) were almost identical in morphology to the smallest specimen although some had incomplete lateral lines. The specialized midventer scales were discernible on males at about 23 mm, and the orange band was present in the spinous dorsal fins of 25-mm specimens. At 27 and 28 mm, scales were lacking only on the nape, and most individuals had completed supratemporal canals. Scales were not present on the nape until specimens reached a standard length of 33 mm.

The pigmentation of *P. phoxocephala* continued to darken throughout life. Older individuals in any particular collection always were slightly darker than the younger ones.

Growth

Standard length frequencies of specimens of *P. phoxocephala* taken from the study area indicated that rapid growth occurred during the first few months of life and the growth rate diminished with age. The growth curve for samples taken from the study area (Fig. 7) showed a continuous average increase in size except during October and November, when the mean standard lengths of two samples averaged less than those of the Septem-

ber sample. This autumn reversal, which also occurred in the study of *P. sciara*, is assumed to be the result of an emigration of the larger fishes from the comparatively shallow raceways (most efficiently sampled) to the deeper channel as winter approached.

Inasmuch as the average size of 12-month-old *P. phoxocephala* specimens was 46 mm, the young fish attained half of their 1st year's growth in about 2 weeks. *Etheostoma gracile* "attained almost half of their 1st year's growth in about 1 week" (Braasch & Smith 1967: 9). The growth rate of the Embarras River *P. phoxocephala* population was faster than that found for the Kaskaskia River population (Thomas 1970:14) and much more rapid than that of the population in Boone County, Iowa (Karr 1963:232). At the end of 1 year's growth, the Embarras River population averaged 45.7 mm in standard length; the Kaskaskia River population averaged 45.3 mm in total length; and the Iowa population averaged 34.1 mm in total length.

There is little indication of sex influence on size.

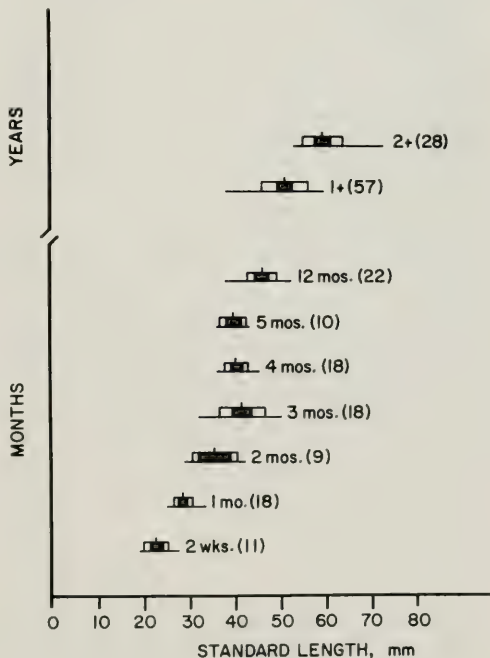


Fig. 7.—Growth of *Percina phoxocephala* in millimeters of standard length. For each sample the horizontal line represents range; the vertical line, mean; the hollow rectangle, one standard deviation to either side of the mean; and the black rectangle, two standard errors to either side of the mean. Numbers in parentheses are specimens measured. Samples of 1- and 2-year-old fish included Embarras River specimens from outside the study area.

Although the largest specimens collected in the study area were males, the differences between male and female mean standard lengths at various ages were not statistically significant. Thomas (1970:13) also found no influence of sex on growth rate.

DEMOGRAPHY

Density

Four specimens of *P. phoxocephala* were taken in the 507 square yards of river quantitatively sampled by an electric seine as described earlier. The sample contained 750 fishes, an average of 1.48 fish per square yard (average depth 30 cm) and one *P. phoxocephala* per 169 square yards. Assuming that, rather than being uniformly distributed in the area sampled, *P. phoxocephala* mainly occupied the gravelly raceway that constituted about one-fourth (127 square yards) of the area, a more realistic figure of one darter per 42.3 square yards of gravel habitat results. Because of the inefficiency of sampling by the electric seine and previous collecting in the area, the figure of one darter per 42.3 square yards may be rather low.

At two sites in the Kaskaskia River, Thomas (1970:6) found more than 200 *P. phoxocephala* individuals per acre of water, which is one darter for approximately 24 square yards of water, almost twice the density of *P. phoxocephala* in the Embarras River. However, at many other sites in the Kaskaskia River, the number of *P. phoxocephala* individuals per acre was smaller than that in the Embarras River study area.

Composition

Of the 238 *P. phoxocephala* collected in the study area, 176 (74 percent) were young-of-the-year, 59 (25 percent) were 1-year-old fish, and 3 (1 percent) were 2-year-old fish (Table 3). No specimens 3 years old or older were examined, and in view of the sharp decrease in numbers in each successive age class, it is doubtful that in the Embarras River many individuals live to 3 or more years of age. Of 25 specimens from Boone County, Iowa, examined by Karr (1963:232), five were 3 years and two were 4 years old.

TABLE 3.—Distribution of sexes and year classes in *Percina phoxocephala* taken from the study area between August 4, 1967 and September 20, 1970.

Sex	Number by Year Class			
	—1	1+	2+	Total
Males	98	38	3	139
Females	72	21	0	93
Too small to sex	6	..	..	6
Total	176	59	3	238

Considerably more males than females were collected, giving a sex ratio of 1.5 males to 1 female. The sex ratio of the 170 young large enough to be sexed was also skewed in favor of the males, although less than that of the total sample (1.4:1). In the small sample from the Kaskaskia River that Thomas (1970:14) used to illustrate growth rate, there were 23 males and 18 females (1.3:1). However, much larger samples are needed to determine the true sex ratio of these populations.

Although the data in Table 3 suggest that *P. phoxocephala* males live somewhat longer than females, 12 of the 28 two-year-old fish examined for the data shown in Fig. 7 were females. If there actually is a skewed sex ratio in the population, more males than females would be expected in any age class, and this factor would obscure any sex influence on longevity.

The largest specimen examined by us was a 78-mm, 2-year-old male collected in the Kaskaskia River on September 6, 1968. Trautman (1957:543) listed the largest Ohio specimen as 4 inches long (approximately 100 mm total length).

Migration

P. phoxocephala exhibited the same annual migratory pattern as that shown by *P. sciara*, i.e., a late fall emigration from and an early spring return to the gravelly raceways (Fig. 8). Unfortunately, the habitat to which the darters emigrated in winter could not be determined. Quiet regions of the river, such as sluggish backwater areas and pools and the deeper portions of

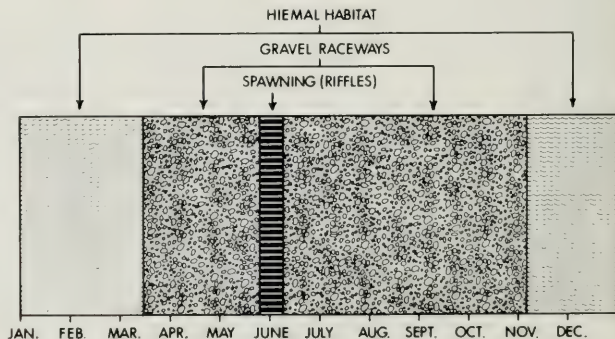


Fig. 8.—The habitats in the Embarras River occupied by *P. phoxocephala* throughout the year. The principal habitat, the gravel raceway, is abandoned during the spawning period and during the colder months of the year.

the channel, were seined, but no darters were found. In February a specimen was collected in the relatively shallow portion of the channel, but its occurrence there was exceptional, and other attempts to collect specimens in the winter months were unsuccessful. *P. phoxocephala* left the raceway areas in November and returned in March or April.

Besides the hial migration, the spring movements into and out of the spawning area involved a large proportion of the population and should be recognized as a breeding migration characteristic of the species. Whether *P. phoxocephala* migrated in and out of tributaries with the change in seasons as *P. sciera* was thought to do is unknown.

Territoriality

Mass movements of the males into the spawning habitat well before the females suggested that the species was territorial during the spawning season. Aquaria used to observe *P. phoxocephala* were probably too small to allow the establishment of territories although males were rather consistently belligerent toward other males.

PHYLOGENETIC RELATIONSHIPS

In his description of *Hadropterus nasutus*, Bailey (1941:1-2) suggested a close relationship with *P. phoxocephala* and *P. oxyrhyncha*. *Percina squamata*, the fourth species in the subgenus *Swainia*, is more generalized and less closely related, but it strongly resembles *P. phoxocephala* in some characteristics, most notably the pigmentation pattern.

Swainia is one of the most primitive subgenera of *Percina*. Generalized characteristics of the subgenus include the modest specialization of the midventral row of scales in the male, lack of pronounced sexual dimorphism, highly pelagic habits, and high meristic counts. Comparisons of data collected during this study and

during the life-history study of *P. sciera* indicate *Swainia* to be somewhat less evolutionarily advanced than the subgenus *Hadropterus*.

Winn (1958b:188) suggested the degree of abatement of the gas bladder to be an indicator of phylogenetic advancement of darters. Page & Smith (1970:11) found *P. sciera* to have a large bladder, averaging approximately 16 percent of the standard length of the fish examined. In eight *P. phoxocephala* specimens the bladder was also large, ranging from 11 to 18 percent and averaging 15 percent of the standard length.

DIET AND FEEDING HABITS

Thomas (1970:8-12) examined the stomach contents of 103 *P. phoxocephala* from the Kaskaskia River, Illinois. He found the predominant food items to be "baetid nymphs, chironomid larvae, and hydropsychid larvae," and noted that certain organisms (e.g., stonefly naiads and elmids beetle adults), although abundant in the darter habitat, were avoided as food items by all four darters he studied. The young fed mainly on midge larvae.

In 45 specimens of *P. phoxocephala* from the Embarras River study area examined for stomach contents (Table 4), midge larvae and pupae, black fly larvae, caddisfly larvae, and mayfly naiads formed over 99 percent of the food items encountered. Less frequent items were amphipods, fish eggs, and terrestrial insects.

The small variety of food items found in *P. phoxocephala* was also found in *P. sciera* studied in the same area. In addition to a similarity in over-all diet, the seasonal variations in the diets of the two species were approximately concurrent; dipterans and mayflies predominated during all seasons, and caddisflies formed a large portion of the diet during the summer (Fig. 9). The correlation between the two fish species in seasonal variations in diet strongly suggests that both fed on whatever insect immatures were available and palatable,

TABLE 4.—Stomach contents of *Percina phoxocephala* of all sizes collected in the Embarras River. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs Examined in Which Each Food Organism Occurred									
	Feb. (1)	Mar. (2)	Apr. (4)	May (4)	June (9)	July (9)	Aug. (4)	Sept. (4)	Oct. (4)	Nov. (4)
Midge larvae, pupae	100	100	25	50	44.4	55.6	50	100	75	50
Black fly larvae	100	...	100	25	22.2	22.2	..	25	..	..
Caddisfly larvae	100	...	25	25	22.2	44.4	25	50	50	..
Mayfly naiads	...	...	75	100	66.7	66.7	..	50	25	50
Miscellaneous	...	...	...	25	...	...	25	..	..	25

Food Organism	Mean Number of Food Organisms Per Stomach									
	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Midge larvae, pupae	5.00	3.00	0.25	2.75	1.89	3.33	1.00	15.75	3.25	0.75
Black fly larvae	1.00	...	15.50	15.50	6.00	0.44	...	0.50	...	...
Caddisfly larvae	1.00	...	0.25	0.25	0.44	2.33	0.25	1.50	1.75	...
Mayfly naiads	...	...	1.25	2.75	4.33	1.00	...	0.50	2.50	0.75
Miscellaneous	...	...	...	0.25	...	...	0.25	...	...	0.25

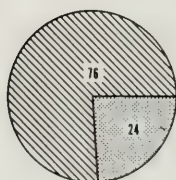
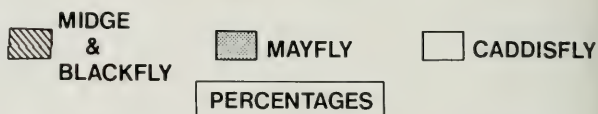
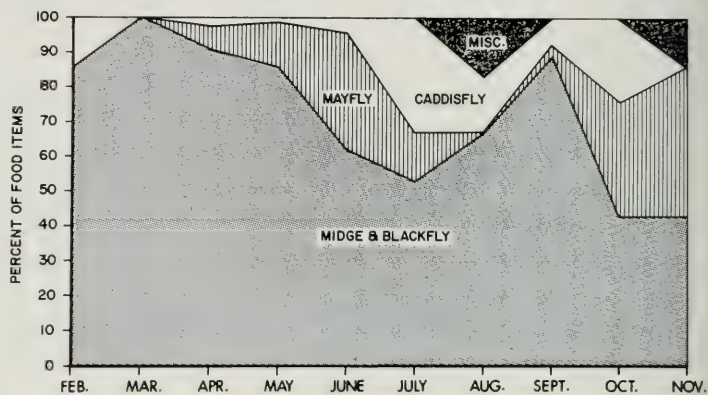
and that the variation was mainly an expression of cycles in insect populations.

The heaviest feeding occurred in May as the spawning season approached. The periods of least feeding

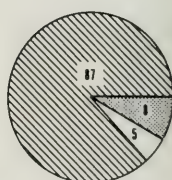
activity were in the months following spawning (July and August) and in the colder months (November, February, and March).

As the darters increased in size, the over-all diet

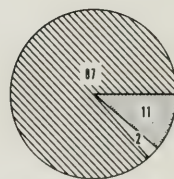
Fig. 9.—Seasonal variation in the diet of *Percina phoxocephala* specimens of all sizes. The percentage of each food item represents its contribution to the total number of items found in all fish examined each month.



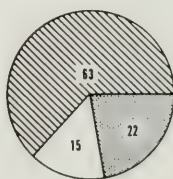
21-30mm
(10)



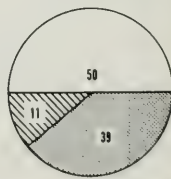
31-40mm
(10)



41-50mm
(10)



51-60mm
(12)



61-70mm
(3)

Fig. 10.—Composition of the diets of five size-classes of *Percina phoxocephala*. Numbers in parentheses are specimens examined.

composition progressed from one dominated by dipteran larvae to include substantially greater portions of the larger mayfly and caddisfly immatures (Fig. 10). The smallest specimen (19 mm) available for dissection contained one mayfly naiad. Aquarium-held darters fed readily on a variety of foods, including fish and shrimp flesh, earthworms, snails, isopods, and tadpoles of *Pseudacris triseriata*.

Some geographic variation in diet is to be expected, although other reports on the food of *P. phoxocephala* have indicated basically the same composition. In a study conducted in Iowa, Karr (1963:234) found mayflies to be the most common food organisms, with dipteran and caddisfly larvae constituting the remainder of the diet. Additional items encountered include dragonfly naiads and water boatmen (Forbes 1880:23; Forbes & Richardson 1920:286; Cross 1967:293).

INTERACTIONS WITH OTHER ORGANISMS

Competition

Observations of *P. phoxocephala* and *P. sciera* for 3 years revealed no overt competition between them or with any other coinhabitants. However, covert competition among species is more difficult to discern, and in field studies can only be suggested in terms of similarities in life histories and niche requirements. *P. sciera* and *P. phoxocephala* share certain ecological characteristics (e.g., similar diets, habitats, breeding habitats) in the Embarras River, and competition between them (and perhaps with other species) may intensify to the point of population limitation in certain seasons of the year. For example, food may become limiting in winter.

Predation

No evidence of predation on *P. phoxocephala* was found in the study area. Concurrent with the life-history studies of the darters, an investigation was conducted on the feeding habits of the most abundant large predator

in the river, *Micropterus punctulatus* (Smith & Page 1969). The only darter remains encountered as food items were those of *Etheostoma nigrum*. Thomas (1970:16) also found no evidence of predation on *P. phoxocephala*.

Parasitism

During the summer and fall, adult and young darters were often parasitized by a small leech, identified by Dr. Marvin C. Meyer as *Piscicolaria reducta* Meyer (Piscicolidae). Darters with leeches attached were collected from late June into November; more than half of those collected in October and November were parasitized by one to eight leeches of various sizes. Attachment was usually to the caudal fin, sometimes to the caudal peduncle or a pectoral fin. In some cases fin rays showed slight damage.

Of 45 *P. phoxocephala* individuals dissected for food analysis, one had one small nematode in its intestines, and another had three nematodes. Another darter of this species from Henry County, Ill., had two small acanthocephalans in its intestines.

Hybridization

The only literature report known to us of natural hybridization involving *P. phoxocephala* is that by Thomas (1970:16) on two specimens of *Percina maculata* x *P. phoxocephala* hybrids from the Kaskaskia River at Sullivan, Ill.

SUMMARY OF LIFE-HISTORY DATA ON *P. PHOXOCEPHALA* AND *P. SCIERA*

A comparison of the life histories of *P. phoxocephala* and *P. sciera* reveals a few ecological and demographic differences and many similarities (Table 5). The differences reflect divergent specialization. The similarities are due, in part, to the relatively close relationship between the two darters and to the fact that both species were investigated in the same study area.

TABLE 5.—Summary of life-history information on Embarras River populations of *Percina phoxocephala* and *P. sciera*.*

Characteristic	<i>P. phoxocephala</i>	<i>P. sciera</i>
Principal habitat	Gravel raceways of moderate-sized rivers	Gravel raceways of moderate-sized rivers
Spawning habitat	Gravel riffles 15-60 cm deep	Gravel riffles 30-90 cm deep
Habitat of juveniles	Gravel riffles	Gravel riffles
Age at reaching sexual maturity	1 year	1 year
Size at reaching sexual maturity	Males about 40 mm; females about 40 mm	Males about 50 mm; females about 40 mm
Sexual dimorphism in spring	Slight in pigmentation	Pronounced in both pigmentation and size
Breeding tubercles	Absent	Absent
Number of mature ova counted	50-720	80-196
Description of egg	1.3 mm in diameter, transparent, adhesive	1.5 mm in diameter, transparent, adhesive
Usual peak spawning period	Early June	Early June
Territoriality	Probable during spawning season	Probable during spawning season
Adult morphology nearly complete	At 3 weeks	At 3 weeks
Influence of sex on growth rate	None	Males grow faster than females
Longevity suggested by study	2+ years	4+ years
Influence of sex on longevity	Males 2+ years; females 2+ years	Males 4+ years; females 3+ years
Maximum size suggested by study	78 mm	108 mm
Sex ratio among young	1.4 males: 1 female	1.1 males: 1 female
Migrations	Breeding; hiemal	Breeding; hiemal; tributarial
Principal diet	Aquatic insect immatures	Aquatic insect immatures

* Supportive data in Page & Smith (1970).

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